Journal of Applied Ecology

From unburnt to salvage logged: quantifying bird responses to different levels of disturbance severity

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Word Count: 8049 words

Running Head: Birds and combinations of fire and logging

ABSTRACT

1. Forests worldwide are increasingly subject to natural and human disturbances, including wildfires and logging of varying intensity and frequency. Understanding how biodiversity responds to different kinds and combinations of natural and human disturbance is critical to enhanced forest management.
2. We completed an eight-year study of bird responses across a spectrum of disturbance types in Australian Mountain Ash (*Eucalyptus regnans*) forests following wildfires in 2009.
3. We found evidence of a gradient in bird species richness over the study duration. It was highest in unlogged and unburned (least disturbed) sites, decreasing through burnt unlogged forest (subject to high or low intensity fire), lower still in logged forest, and lowest in the most disturbed sites (subject to salvage logging without island retention). Retention of uncut islands within logged areas increased bird species richness above that found in areas that had been clearcut.
4. The greatest rate of increase per year after disturbance in bird species richness was on sites burnt by high severity fire but which were not subject to any form of logging. The level of disturbance affected the composition of the bird assemblage. Sites that were unlogged and unburned were more likely to support species that were larger, more mobile, and nested at greater heights above the ground.
5. *Synthesis and applications*. All forms of logging on burned sites impaired recovery in bird species richness relative to sites subject to high severity fire. Alterations in stand structure and plant species composition (and hence modification in bird habitat suitability) due to logging are the most likely reasons for reduced bird species richness and delayed patterns of recovery. This study highlights the importance for native bird species of retaining patches of unlogged forest not only within otherwise

clearcut forest, but also in areas that are burned and subject to salvage logging. We therefore suggest that the adoption of retention harvesting be expanded to include stands disturbed by wildfires.

KEYWORDS: forest birds, Mountain Ash, natural disturbance, salvage logging, south-eastern Australia, variable retention harvest systems, wildfire, fire, species richness

INTRODUCTION

Disturbances such as fire, windstorms and floods can have a major influence on both natural and human-modified ecosystems and affect the abundance and diversity of species, nutrient and energy cycling, biomass accumulation, hydrological regimes and other key ecosystem processes (Sousa 1984; Swanson *et al.* 2011; Fairman, Nitschke & Bennett 2016; Pulsford, Lindenmayer & Driscoll 2016). The severity, intensity or frequency of natural disturbance regimes can be altered directly and indirectly by human activities (Bradley, Hanson & DellaSala 2016; Parisien *et al.* 2016) such as patterns of land use (Thompson, Spies & Ganio 2007; Cochrane & Laurance 2008; Taylor, McCarthy & Lindenmayer 2014), climate change (Westerling *et al.* 2006; Abatzoglou & Williams 2016) and the establishment of invasive species (Setterfield *et al.* 2010; Johnstone *et al.* 2016; Jones *et al.* 2016). Thus, there can be additive or interactive effects of human and natural disturbances in biodiversity and key ecosystem processes (Buma 2015; Kishchuk *et al.* 2015; Lindenmayer, Thorn & Banks 2017). Understanding how biodiversity responds to different combinations of disturbances is critical to developing prescriptions that underpin the effective management of natural resources (Frelich 2005; Driscoll *et al.* 2010; Leverkus & Castro 2017; Lindenmayer, Thorn & Banks 2017).

A potentially severe form of perturbation in forests is salvage logging in which trees damaged by natural disturbance are harvested in an attempt to recover some of their economic value (Cobb *et al.* 2011; Fraver *et al.* 2017; Leverkus & Castro 2017). Salvage logging is widespread and its use is increasing (Thorn *et al.* 2017), likely as a result of the increase in large-scale intensive natural disturbances globally (Seidl *et al.* 2014). There has also been a rapid increase in the number of studies of salvage logging but many lack data on the effects of some important combinations of natural and human disturbance (D'Amato *et al.* 2011; Thorn *et al.* 2017; but see Cobb *et al.* 2011; Kishchuk *et al.* 2015). This includes contrasts between salvage logged areas and places subject to conventional harvesting methods such as clearcutting, but particularly lower intensity silvicultural systems like variable retention harvesting (sensu Gustafsson *et al.* 2012; Fedrowitz *et al.* 2014).

Here we quantify the response of forest birds across a range of disturbance types, resulting from fire, logging and a combination of both in the wet Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-eastern Australia. Large areas of the study region burned in wildfires in 2009. This event, coupled with subsequent post-fire salvage logging operations and ongoing conventional clearcut logging in unburned forest, provided a unique opportunity to establish a comparative study of disturbance effects (Fig. 1; Table 1). Our study design included replicate sites that were: **(1)** unburned and unlogged, **(2)** burned at low severity in 2009, **(3)** burned at high severity in 2009, **(4)** subject to conventional clearcut logging operations (i.e. unburned stands were clearcut), **(5)** subject to variable retention harvesting (in which islands of uncut green forest were retained within cutblocks), **(6)** subject to conventional post-wildfire salvage logging, and, **(7)** had been salvage logged but with burned islands of forest retained within the cut area (Fig. 1). This last treatment was an extension of the island retention approach typically employed in conventional green forest variable retention harvesting systems (Fedrowitz *et al.* 2014) but applied in a salvage logging context. Our range of treatments therefore facilitated contrasts in bird responses not only between conventional post-fire salvage logging and conventional clearcut logging but also contrasts among sites where variable retention harvesting was deployed in burned versus unburned forest. Our study design also enabled us to determine whether the effects of salvage logging were more substantial than the effects of clearcut logging alone plus the effects of high-severity fire alone. That is, in quantifying the effects of salvage logging on bird biota, we sought evidence for both additive effects of high severity fire and subsequent clearcut logging as well as interactive impacts (sensu Foster *et al.* 2016) between these two kinds of disturbance.

We examined four components of bird response – bird species richness, the composition of the bird assemblage, the occurrence of individual bird species, and bird life history attributes (as part of testing performance filtering hypothesis and functional diversity theory; (Mouillot *et al.* 2012; Aubin *et al.* 2016)). We motivated our investigation by posing two key questions to quantify the three components of biotic response:

Question 1. *Are birds affected by different combinations of natural and human disturbance?* At the outset of this investigation, we postulated that bird species richness and the detection frequency of individual bird species would be lowest in areas subject to conventional salvage logging and highest in unlogged and unburned sites (see Fig. 1). We also postulated that the composition of the bird assemblage would vary between sites subject to different disturbances with some kinds of species (characterized by particular life history traits) being absent from intensively disturbed areas.

The broad focus of Question 1 was on cross-sectional contrasts in bird responses between sites subject to different levels of disturbance severity. However, our work entailed documenting changes in bird responses between 2009 and 2016, thereby providing an opportunity to quantify **temporal** patterns on different kinds of sites. Hence, the second question in our investigation was:

Question 2. *Does the temporal response of bird species richness and individual species vary among sites subject to different kinds of disturbance?* We postulated that, relative to unlogged and unburned sites, the recovery of bird species richness would be slowest in salvage logged sites with no island retention that were those most heavily perturbed (Fig. 1). This was because such sites lack critical structural elements (e.g. dead standing trees) and have the most depauperate vegetation communities of all the forest stand categories that we studied (Lindenmayer & Ough 2006; Blair et al. 2016). In our study, we used our unburnt and unlogged sites as 'benchmarks' to evaluate the recovery of disturbed sites (Fig. 1). While a small number of bird species in this forest appear to prefer early post-fire conditions (e.g. the Flame Robin *Petroica phoenicea*; (Lindenmayer et al. 2014)), no species occurs exclusively under early successional conditions so our unburnt and unlogged sites were considered an appropriate benchmark for recovery of species richness.

MATERIALS AND METHODS

Study area

Our study area was the Mountain Ash forest in the Toolangi, Marysville and Powelltown districts of the Central Highlands of Victoria, south-eastern Australia (Fig. 2). Stand-replacing fire is one of the predominant forms of natural disturbance in Mountain Ash forests leading to stands of broadly uniform age (Smith *et al.* 2016). We constrained our study to one age class of forest – stands that were 70 years old at the time of the 2009 wildfires, having regenerated after previous wildfires in 1939. This was to avoid confounding disturbance treatment effects with forest age effects given that different stand ages of Mountain Ash forest support different faunal assemblages, including birds (Loyn 1985; Lindenmayer *et al.* 2009). In addition, 1939 regrowth forest was the most extensive age class in the Mountain Ash ecosystem at the time of the fires (Burns *et al.* 2015) and it is where almost all timber harvesting activity presently takes place (Flint & Fagg 2007). Old growth stands (which are excluded from logging) are now rare in Mountain Ash ecosystems and constitute approximately 1.2% of the extent of this vegetation type in the Central Highlands region of Victoria (Lindenmayer *et al.* 2012).

Our study included three levels of fire severity at a site as determined from on-the-ground measurements of vegetation 1-2 months directly following the 2009 fire. Unburned sites were those which were not subject to fire in 2009. Low severity sites were those where the ground was damaged but the understorey and overstorey remained intact. High-severity sites were those in which plants in the ground, shrub and understorey layers were killed and crowns of overstorey trees consumed.

Experimental design and disturbance classes for contrast

The design for this study took advantage of three major studies that ran concurrently from 2009-2016 in which the surveys for birds all employed broadly similar field sampling protocols (by the same field researchers) (see below).

The first investigation was a long-term study of the occurrence of birds on sites that were dominated by 1939 regrowth at the time of the 2009 fires. The study included sites burned at high severity in the 2009 fires, sites burnt at low severity in 2009, and sites that remained unburnt in 2009 (Lindenmayer *et al.* 2014) (Table 1).

Our second study was a blocked and replicated experiment designed specifically to contrast vertebrate response (including birds) to variable retention harvesting (Lindenmayer *et al.* 2015). The experiment comprised three key treatments in 1939 regrowth forest: **(1)** unlogged forest, **(2)** forest subject to conventional clearcutting (i.e. no island retention), and **(3)** forest subject to variable retention harvesting in which islands of unlogged forest were retained. The treatments were implemented within an experimental block, with the blocking structure replicated, giving a total of 15 sites (Table 1).

Our third study was a blocked and replicated salvage logging experiment initiated immediately following the 2009 wildfires. It was designed to have broad parallels with the experiment on variable retention harvesting, except in a post-fire logging setting. The salvage logging experiment comprised 20 sites in three treatments: **(1)** burned but unlogged sites, **(2)** conventionally salvage logged sites (with no stand retention), and **(3)** salvage logged areas with island retention (Table 1).

In the case of salvage logged areas, all trees were killed by high-severity fire – in part because salvage logging is restricted (by regulation and codes of practice) only to those areas subject to very high-severity fire. In the case of conventionally clearcut areas, the only green trees remaining within cutover areas are in the retention islands – all standing trees in the remainder of the cutblock were logged (i.e. cut down). The size of conventionally logged and salvage logged cutblocks varied from 15-40 ha (as per Codes of Practices in these forests). The area of Mountain Ash forest burned in the 2009 fires exceeded 72 000 ha (Cruz *et al.* 2012).

Bird survey protocols

We conducted bird surveys annually between 2009 and 2016 with surveys completed in November/early December which is the breeding season for the majority of species and when summer migrants have arrived. Our first surveys in 2009 occurred after disturbance by fire or logging. Our standardised survey protocol was repeated five-minute point interval counts (sensu Pyke & Recher 1983; Ralph, Sauer & Droege 1983). For all broad site types in this study and in each year of sampling, we surveyed each site on two different days to account for day effects (Field, Tyre & Possingham 2002). The count on the first day was completed by a different observer than the count on the second day to account for observer heterogeneity (Cunningham *et al.* 1999; Lindenmayer, Wood & MacGregor 2009). We conducted surveys between sunrise and 9.30 am and did not complete counts on days of rain, fog or high winds.

For the 54 sites within the long-term monitoring study, we established a 100 metre transect with permanent plots at 0 m, 50 m and 100m points. We did not assume that individual counts at the three points on the same site were independent. We limited our surveys to birds detected within 50 m of a plot point on a given transect. This was to ensure that the birds recorded were within the particular disturbed sampling unit in question. Standardizing the size of the area sampled meant that it was possible to robustly compare counts made across the different studies which together comprised our study (see below).

We also established permanent plots in the variable retention harvesting and salvage logging experiments. The variable retention harvesting experiment entailed establishing a permanent plot within a retention island with only birds recorded within 50 m of the centroid of the plot to ensure that only individuals wholly within the island were counted. The islands were a minimum of 50 metres apart (and separated by clearcut forest). There were three plots, one for each of the three islands that had been retained on the cutblock. A similar protocol was used for the salvage logging experiment in which three islands of uncut forest (which had been burned in the preceding wildfire) were retained and a permanent plot was established within each island. Again, only birds within 50 m of the centroid of the plot were recorded to ensure that only individuals wholly within the island were counted. We did not assume that individual counts at the plot points within a site were independent. For sites subject to conventional clearcutting and conventional salvage logging, we positioned our permanent 50 m survey plots in the same spatial configuration as for the logged areas subject to the variable retention harvesting and salvage logging experiments.

Bird life history attributes

We compiled data on bird species traits to explore relationships between species' identities on sites subject to different kinds of disturbances and particular kinds of life-history attributes (see Supporting Information Table S1; Lindenmayer *et al.* 2018). We summarized data on body mass and life history traits (movement, diet, and foraging substrate) (Handbook of Australian and New Zealand Birds 1990-2007; BirdLife Australia 2014). These traits are thought to reflect the ability of species to respond to environmental change (Luck *et al.* 2012).

Statistical analyses

We fitted hierarchical generalized linear models (HGLMs) (Lee, Nelder & Pawitan 2006) to our data on bird species richness using quasi-Poisson distributions with a logarithmic link and a gamma distribution with a logarithmic link for random site effects (see Bolker *et al.* 2009). We used a logarithmic link for the fixed effects because we considered that the effects would be approximately multiplicative. We used the conjugate distribution for the random effects for ease of computation and interpretation.

We used Wald tests to quantify the significance of terms included in the HGLMs. We fitted models which included the disturbance categories as a single factor together with the interaction with the logarithm of the number of years since the 2009 fire plus one, as well as models in which we treated burn severity, the logging treatment and the study identity as separate factors.

Our data for individual species were detection frequencies; that is, the number of individual point counts at a site (out of a maximum of six in any given year – 3 plots per site, surveyed twice by a different observer on a different day) in which a given species was recorded. We fitted hierarchical generalized linear models to detection frequency data for individual species. We used a quasi-binomial distribution with a logit link and a beta-distribution with a logit link for the random site effect. This model assumes that fixed effects are additive on the log odds scale and, as for species richness, we used the conjugate distribution for the random effects. We restricted our analyses to the 22 individual species for which there were detections for 40 or more site-year combinations and at least 60 detections in total (Table S2). Species with fewer detections than this had insufficient data to provide reliable results.

We used canonical correspondence analysis (ter Braak 1986; Greenacre 2007) to investigate the effects of disturbance and year on the species assemblage. To avoid distortion of our results by relatively rare species, only species with more than 20 detections (N=35) were included in canonical correspondence analysis. We fitted linear regressions of the resulting species scores on a number of bird life history characteristics. We also tested the effect of year and disturbance in the year by disturbance scores using the interaction as the error term.

We completed statistical analyses using Genstat for Windows Release 18.2 (VSN International 2015) and R version 3.2.2 (R Core Team 2016).

RESULTS

Differences in species richness in response to different combinations of disturbance

Our analyses revealed a highly significant (χ^2_9 = 206.2, P < 0.001) gradient in bird species richness with unburned and unlogged sites supporting significantly greater numbers of species (11.8 ± 0.45SE) relative to sites subject to conventional salvage logging operations (3.8 ± 0.43SE) (Fig. 3). Values for mean bird species richness in other categories of sites were generally intermediate between the two extremes, with the highest on unlogged sites (*viz*: those subject to low and high severity fire) and lowest where various kinds of logging operations had occurred (Fig. 3). We found no statistical evidence to suggest the impacts of salvage logging on bird species richness were significantly greater than an additive combination of the effects of high severity fire alone plus and clearcut logging alone. That is, our data contained no evidence of a significant interaction between high severity fire and clearcut logging on bird species richness.

Temporal changes in species richness in response to different combinations of disturbance

There were significant (χ^2_9 = 87.2, P < 0.001) differences in the estimated annual rates of change in mean bird species richness for the different disturbances (Fig. 3). There also was evidence of a positive change in mean bird species richness on sites subject to high levels of disturbance (Fig. 3).

We found marked interspecific differences in response to the range of disturbances in our study (Fig. 4). The Crescent Honeyeater (*Phylidonyris pyrrhopterus*) (Fig. 4) (χ^2_9 = 24.5, P = 0.004), and the Eastern Yellow Robin (*Eopsaltria australis*) (Supporting Information Fig. S1) (χ^2_9 = 25.6, P = 0.002) were among the relatively few individual species which exhibited a pattern of response similar to that identified for mean species richness (i.e. detection frequency was highest on unlogged and unburnt sites and lowest on conventionally salvaged logged sites (see Fig. 2). The detection frequency of the Flame Robin was highest on sites burned at high severity (Fig. 4) (χ^2_9 = 55.0, P < 0.001) whereas it was highest for the Eastern Spinebill (*Acanthorhynchus tenuirostris*) (χ^2_9 = 51.0, P < 0.001) on variable retention logged areas where retained patches remained unburned (Fig. 4). Several individual species were significantly affected by fire, with adverse effects identified for the Brown Thornbill (*Acanthiza pusilla*) (χ^2_2 = 10.3, P = 0.006), Crescent Honeyeater (χ^2_2 = 15.4, P < 0.001), Eastern Spinebill (χ^2_2 = 33,3, P < 0.001), Eastern Whipbird (*Psophodes olivaceus*) (χ^2_2 = 11.9, P = 0.003), Eastern Yellow Robin (χ^2_2 = 14.0, P < 0.001), Rose Robin (*Petroica rosea*) (χ^2_2 = 34.9, P < 0.001), Rufous Fantail (*Rhipidura rufifrons*) (χ^2_2 = 18.8, P < *0.001*) (Fig. S1). More complex effects were found for other species; for example, the detection frequencies of the Silvereye (*Zosterops lateralis*) (χ^2_{82} = 15.6, P < 0.001) and Golden Whistler

(*Pachycephala pectoralis*) (χ^2_2 = 36.2, P < 0.001) were highest on severely burned sites and lowest on sites subject to low severity fire (Fig. S1). As in the case of in quantifying salvage logging impacts on bird species richness, we found no evidence of a significant interaction between high severity fire and clearcut logging for any individual bird species.

Temporal changes in individual species in response to different combinations of disturbance

We identified marked inter-specific differences in post-disturbance temporal response of bird species (Fig. 4, Fig. S1). The detection frequency of several bird species increased significantly during the eight years of this study including the Brown Thornbill (χ^2_1 = 23.1, P <0.001), Olive Whistler (*Pachycephala olivacea*) (χ^2_1 = 5.8, P =0.016), Pilotbird (*Pycnoptilus floccosus*) (χ^2_1 = 15.4, P <0.001), and White-browed Scrub-wren (*Sericornis frontalis*) (χ^2_1 = 23.1, P <0.001). The reverse effect was identified for the Rufous Fantail (χ^2_1 = 4.2, P =0.041), and Spotted Pardalote (*Pardalotus punctatus*) (Fig. S1) (χ^2_1 = 5.4, P = 0.023) (Fig. S1).

Response of the bird assemblage to different combinations of disturbance

In the canonical correspondence analysis, the site by year terms accounted for 20% of the variation, and the first two components accounted for 4.5% and 2.0% of the variation respectively. This suggests that factors other than disturbance have a major effect on species composition. A plot of the types of disturbance as represented by the first two components of the canonical correspondence analysis averaged over years was characterised by a gradient from severely burnt sites in the top left to unburnt sites in the bottom right of the diagram (Fig. 5). A second axis from the canonical correspondence analysis represented a somewhat weaker gradient from logged to unlogged forest (Fig. 5). Fig. S2 shows the locations in the first two dimensions for the 35 most common individual bird species and it suggests the composition of the bird assemblage is related primarily to fire. Two species in particular respond positively to fire, the Flame Robin and the Superb Fairy Wren. In addition, we identified significant relationships between the second component of the canonical correspondence analysis and life history attributes which included positive effects on the component scores of nest height ($F_{1,33}$ = 5.6, P = 0.024), wing length ($F_{1,33}$ = 5.3 P = 0.028) and dispersal ratio ($F_{1,32}$ = 5.4, P = 0.027). This analyses indicated that bird species which nested at greater heights above the ground, were larger, or were more mobile were more likely to occur in unlogged forest.

DISCUSSION

Bird responses to different combinations of disturbance

The first key question in our study was: *Are birds affected by different combinations of natural and human disturbance?* Consistent with predictions at the outset of this investigation (see Fig. 1), we uncovered strong evidence of a gradient in bird species richness congruent with differences in the increasing intensity of disturbance from unlogged, unburnt forest through to conventionally salvage logged forest (Fig. 1 and Fig. 3). Conventionally salvage logged sites supported approximately 25% of the levels of bird species richness found on unlogged, unburned sites with such differences characterizing our study not only at its inception in 2009 but also eight years later (Fig. 3).

In comparison with unburned and unlogged sites, we found that levels of bird species richness were highest in areas with increased amounts of the original stand remaining after disturbance, both following fire (i.e. stands burned at low severity support more of the original stand relative to stands burned at high severity), and logging (where variable retention harvesting methods maintain more of the original stand compared to clearcutting) (Fig. 3). Areas subject to clearcutting and salvage logging supported fewer bird species than stands where variable retention harvesting was employed. This result was broadly consistent with the findings of other empirical studies that have explored bird responses across a range of kinds of disturbance (e.g. Barlow *et al.* 2006) as well as global meta-analyses on variable retention harvesting systems which demonstrated that species richness is generally greater with increasingly levels of stand retention (Fedrowitz *et al.* 2014; Thorn *et al.* 2017). Across the spectrum of sites in our study, stands burned at low or high severity supported higher bird species richness than sites subject to variable retention harvesting (including those that were not subsequently burned as well as those that were burned in 2009) (Fig. 3). Thus, our results for bird species richness indicate that all forms of logging reduced bird species richness relative to that quantified for both burned (but unlogged) sites as well as unburned and unlogged sites (Fig. 3).

We suggest that the significant reduction in bird species richness on sites subject to the most severe form of perturbation (i.e. conventional salvage logging) is likely due to changes in vegetation plant species composition, loss of diversity and reduction in other key stand structural elements (e.g. large old trees) typically associated with this form of harvesting (e.g. Foster & Orwig 2006; D'Amato *et al.* 2011; Blair *et al.* 2016; Fraver *et al.* 2017; Leverkus & Castro 2017).

The pattern we identified for species richness was not replicated for the detection frequencies of most individual bird species. Rather, we found evidence of highly species-specific responses to disturbance (Fig. 4, Fig. S1) which highlights the importance of a broader examination of relationships between the intensity of disturbance and bird life history relationships as outlined below.

Temporal changes in individual species responses to different combinations of disturbance

At the outset of this investigation, we predicted the recovery of bird species richness would be slowest on sites subject to the most severe kinds of disturbance (Fig. 1). We found that the greatest rate of post-disturbance recovery in species richness was on sites subject to high severity fire (Fig. 3). We acknowledge that rates of recovery are not independent of the degree of reduction in species richness after initial disturbance. That is, there will be limited "recovery" on unburnt and unlogged sites because there was never a decline. Rapid recovery in species richness on sites subject to high severity fire is, in part, a function of the substantial initial reduction in species richness at the time of disturbance, although overall richness still did not approach that of unburnt unlogged sites. Part of the explanation for relatively rapid recovery may be related to high-severity fire that leads to dense natural regeneration around dead trees from the previous fire-killed stand (Blair *et al.* 2016; Smith *et al.* 2016). Stands characterized by rapid regeneration in vegetation structure coupled with numerous dead and burned standing trees may, in turn, provide an array of suitable habitat niches for a range of bird species. Notably, such patterns of positive response in bird species richness were not as pronounced on logged sites. This included areas subject to salvage logging (both conventional salvage logging and those subject to salvage logging but with stand retention) as well as sites which had been conventionally clearcut or subject to variable retention harvesting system (Fig. 3). This suggests that all forms of logging impair the rate of bird recovery relative to that quantified for sites subject to high severity fire. Notably, there might there be an upper bound on recovery rate following wildfire if logging in the surrounding burned forest reduces source populations of birds, akin to the landscape trap hypothesis that has been proposed for Mountain Ash forests (Lindenmayer *et al.* 2011). However, detailed medium to long-term source-sink studies would be required to quantify such risks to bird population recovery (if they exist).

Limitations of the study

We acknowledge that there some limitations to our study. First, limited data prevented us from analyzing results for rare species, although we recognize there are very few bird species of conservation concern in Mountain Ash forests. For example, the Flame Robin (which is an early successional responder in our study system) is under threat in other Australian ecosystems (Montague-Drake, Lindenmayer & Cunningham 2009). A second limitation was that we combined datasets from three different studies. However, we included study identity in the modeling and the same field staff employed similar sampling methods within one forest type and the same aged forest in that forest type.

Disturbance and bird life history relationships

Consistent with the performance filtering hypothesis and functional diversity theory (Mouillot *et al.* 2012; Aubin *et al.* 2016), we found evidence that disturbance (particularly fire) affected particular functional groups of birds (and therefore the composition of the bird assemblage). Birds which nested at greater heights in the vegetation, or were larger, or were less mobile were more likely to be associated with unburned forest. The reasons for these results remain unclear. However, it is likely that the short regenerating trees are unsuitable for birds that nest at greater heights. In addition, less mobile (e.g. resident) species may take a prolonged period to recolonize intensively perturbed areas from which they have previously been displaced.

Implications for conservation and management

Our data suggest that both clearcutting and variable retention harvesting have different effects on birds relative to wildfire (including high-severity fire). The most intense forms of disturbance examined (conventional salvage logging with no island retention) led to the most substantial reduction in bird species richness and also impaired post-disturbance recovery in bird species richness (Fig. 3). Earlier work in Mountain Ash forests highlighted the extent to which salvage logging operations can alter potential nesting and foraging habitat for other groups of animals like arboreal marsupials such as through depleting key elements of stand structure like large old hollow-bearing trees (Lindenmayer & Ough 2006) and resprouting understorey plants (e.g. tree ferns) (Blair *et al.* 2016). These impacts suggest a need to limit the amount of salvage logging in the event of future high-severity wildfires in Mountain Ash forests.

There have been proposals to increasingly shift away from clearcutting to retention harvesting in many forest types globally (Gustafsson *et al.* 2012). The results of this study suggest that retention harvesting policies and practices need to be extended beyond green (previously undisturbed) forests to include those that are naturally disturbed (e.g. by fire) and potentially subject to salvage logging. In addition, we suggest it is critically important to ensure that burned areas remain unlogged and are included in the design and implementation of reserves so that protected areas capture the variability of forest conditions and bird communities in a manner that allows for recovery from natural disturbances to proceed unimpeded by post-fire timber harvesting (see DellaSala *et al.* 2015; DellaSala *et al.* 2017).

AUTHORS' CONTRIBUTIONS

DBL, LM and DB conceived the ideas, designed methodology, and collected the data; JW and DBL analysed the data; DBL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This study was supported by grants from the Australian Research Council, the Government of Victoria (Department of Environment, Land, Water and Planning; Parks Victoria) and the Graeme Wood Foundation. We thank Mason Crane, Dan Florance, Chris MacGregor, Damian Michael, Sachiko Okada and Thea O'Loughlin for assistance in gathering data on birds. Comments from Jos Barlow, Sharif Mukul, Dominick DellaSala and three anonymous referees greatly improved an earlier version of the paper.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository doi:10.5061/dryad.24t5j04 (Lindenmayer *et al.* 2018).

SUPPORTING INFORMATION

Table S1. Summary of the life history and morphological traits used in the analysis, and the relationship of these traits with environmental change.

Table S2. Number of detections and number of site x year combinations with birds present for the most common species.

Fig. S1. Estimated effects of disturbance on percentage detection frequency in 2009 and 2016 for 18 individual bird species.

Fig. S2. First two components from canonical correspondence analysis showing locations in multi-dimensional space for the 35 most common bird species.

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Fig. 1. Part A. Conceptual model of types of fire and logging-related disturbances and predicted levels of bird species richness in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia. The spectrum of site types include the *de facto* benchmark unlogged and unburned sites (denoted UD) as the least disturbed areas through to our hypothesized most severely disturbed sites (salvage logged [SC]), salvage logged sites with island retention [denoted SI]). Conventional clearcut areas and sites subject to variable retention harvesting are denoted CC and VR, respectively. **Part B.** Postulated temporal responses in bird species richness in relation to different types of fire and logging-related disturbances

Fig. 2. The location of the study region in the Central Highlands of Victoria, south-eastern Australia.

Fig. 3. Estimated bird species richness in 2009 and 2016 on sites subject to different kinds of disturbance ranging from sites that were unburned and unlogged (UD) to sites subject to conventional salvage logging following the 2009 wildfire (denoted SC). Other codes for site types are given in Table 1 and Fig. 1. The lines above the bars in the figure show the estimated standard errors of the difference between 2009 and 2016 for each of the disturbances. Bird surveys were completed in each year from 2009 and species richness is shown only for the start (2009) and end (2016) of the study.

Fig. 4. Estimated effects of disturbance on percentage detection frequency in 2009 and 2016 for five individual bird species. Response patterns for other individual species of birds are shown in Fig. S1 in the supplementary material. The lines above the bars in the figure show the estimated standard errors of the difference between 2009 and 2016 for each of the disturbances. Bird surveys were completed in each year from 2009 and a subset of individual species responses are shown only for the start (2009) and end (2016) of the study.

Fig. 5. First two components from canonical correspondence analysis showing scores (and therefore locations in multi-dimensional space) for the years in this study and ten types of disturbance examined in this study (see Table 1).

Table 1. Summary of the broad site types in the study of bird responses to different combinations of disturbances in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia. All sites were regrowth from the 1939 wildfires in 2009 when parts of the study region were burned or when they were logged. Standardizing the age class in the study avoided confounding between stand age effects, biotic responses, and various kinds and combinations of disturbances. Not all sites could be surveyed in any given year and the final column in the table provides information on the number of surveys of sites across the duration of the study.

Site type	**Description and associated citations**	**Abbreviation**	**No. of sites**	**No. of site x year combinations**
Undisturbed (Unlogged, unburned)	Forest regenerating after the 1939 wildfires which have remained unlogged and unburned since then	UD	26	171
Low severity fire*	1939 regrowth forest that was burned at low severity in the 2009 fire and was not subject to subsequent salvage logging	LS	8	55
High severity fire*	1939 regrowth forest that was burned at high severity in the 2009 fire but was not subject to subsequent salvage logging	HS	20	77

Variable retention harvesting with island retention, no wildfire in 2009	1939 regrowth forest that was subject to variable retention harvesting between 2006 and 2009 in which islands of forest of 0.5-1.5 ha in size were retained with 15-40 ha cutblocks.	VR	4	20
Conventionally clearcut forest, (with no island retention and no wildfire in 2009)	1939 regrowth forest that was subject to clearcutting between 2006 and 2009 and not subject to wildfire in 2009	CC	2	5
Conventionally clearcut forest, high severity fire in 2009	1939 regrowth forest that was subject to clearcutting between 2006 and 2009, but then burned at high severity in 2009 fires	CC+HS	1	4
Variable retention harvesting with island retention, low severity fire in 2009	1939 regrowth forest that was subject to variable retention harvesting between 2006 and 2009 in which islands of forest of 0.5-1 ha in size were retained with 15-40 ha cutblocks but then burned at low severity in the 2009 fires	VR+LS	3	11

Variable retention harvesting with island retention, high severity fire in 2009	1939 regrowth forest that was subject to variable retention harvesting between 2006 and 2009 in which islands of forest of 0.5-1 ha in size were retained with 15-40 ha cutblocks but then burned at high severity in the 2009 fires	VR+HS	5	24
Conventional salvage logging	1939 regrowth forest that was burned at high severity in the 2009 fires and subject to conventional salvage logging in which the entire damaged stand was clearcut	SC	7	40
Modified salvage logging with island retention	1939 regrowth forest that was burned at high severity in 2009 and then subject to modified salvage logging in which islands of burned forest of 0.5-1 ha in size were retained s	SI	13	64

*Fire severity was determined from on-the-ground measurements of vegetation 1-2 months directly following the 2009 fire (see text).

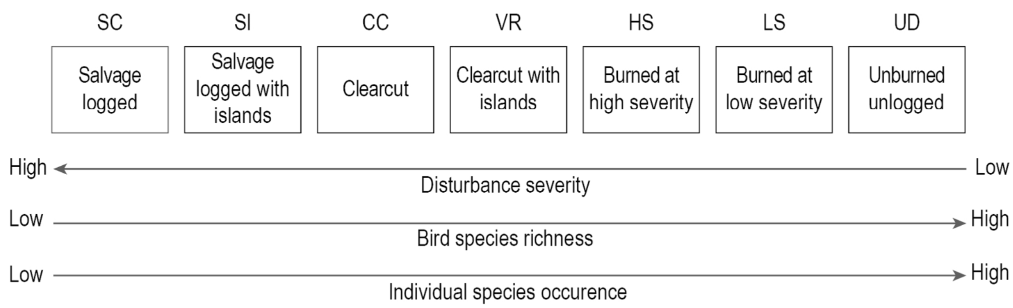

Fig. 1. Part A. Conceptual model of types of fire and logging-related disturbances and predicted levels of bird species richness in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia. The spectrum of site types include the de facto benchmark unlogged and unburned sites (denoted UD) as the least disturbed areas through to our hypothesized most severely disturbed sites (salvage logged [SC]), salvage logged sites with island retention [denoted SI]). Conventional clearcut areas and sites subject to variable retention harvesting are denoted CC and VR, respectively. Part B. Postulated temporal responses in bird species richness in relation to different types of fire and logging-related disturbances

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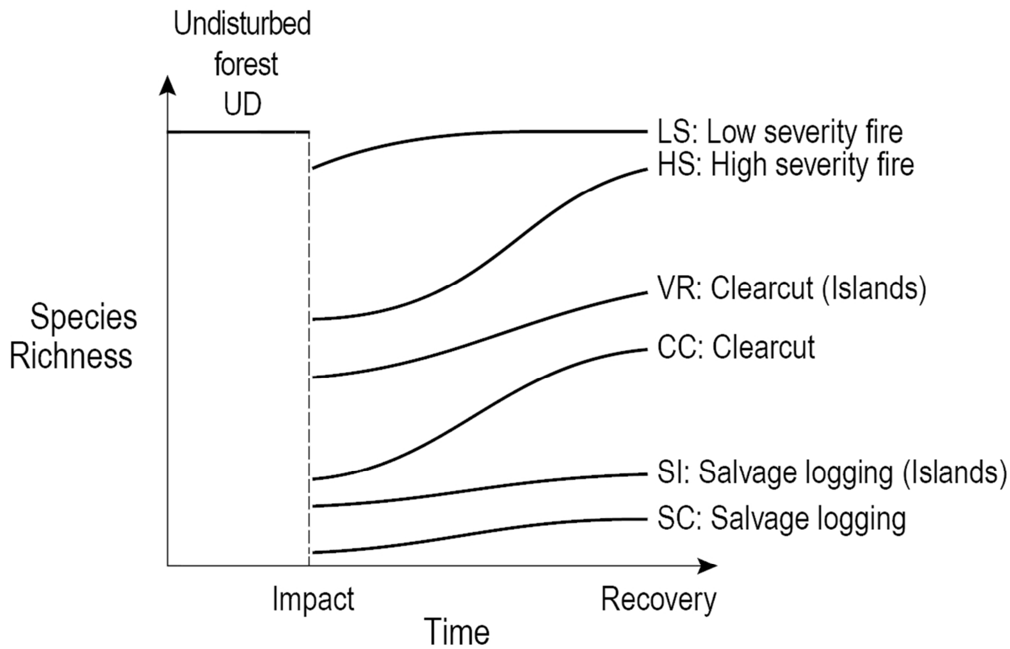

Fig. 1. Part A. Conceptual model of types of fire and logging-related disturbances and predicted levels of bird species richness in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia. The spectrum of site types include the de facto benchmark unlogged and unburned sites (denoted UD) as the least disturbed areas through to our hypothesized most severely disturbed sites (salvage logged [SC]), salvage logged sites with island retention [denoted SI]). Conventional clearcut areas and sites subject to variable retention harvesting are denoted CC and VR, respectively. Part B. Postulated temporal responses in bird species richness in relation to different types of fire and logging-related disturbances

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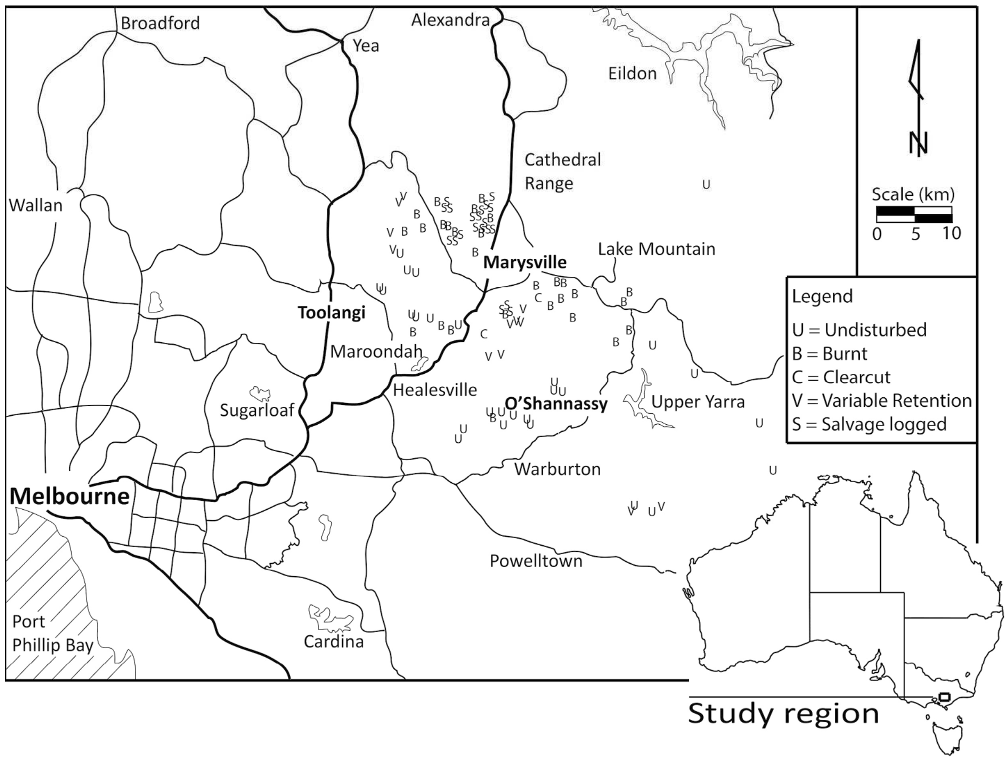

Fig. 2. The location of the study region in the Central Highlands of Victoria, south-eastern Australia.

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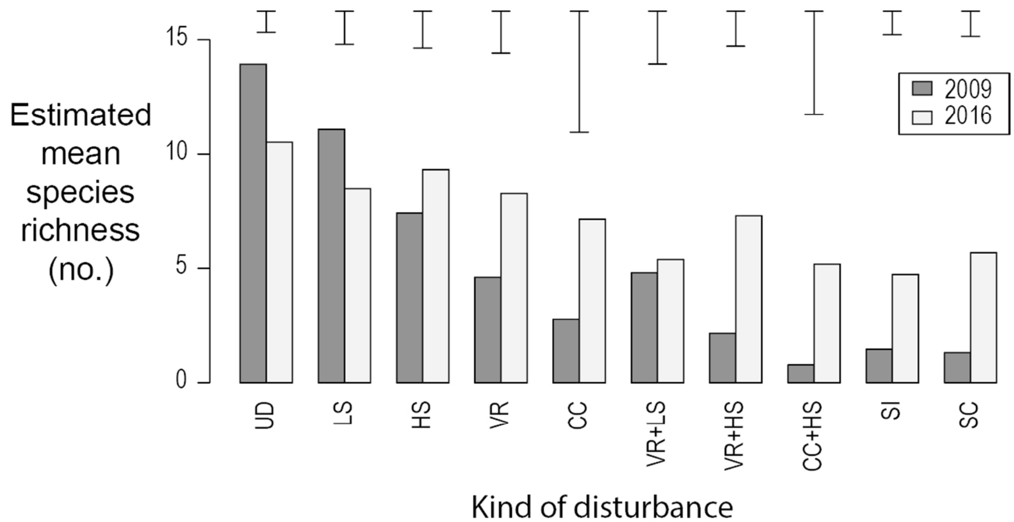

Fig. 3. Estimated bird species richness in 2009 and 2016 on sites subject to different kinds of disturbance ranging from sites that were unburned and unlogged (UD) to sites subject to conventional salvage logging following the 2009 wildfire (denoted SC). Other codes for site types are given in Table 1 and Fig. 1. The lines above the bars in the figure show the estimated standard errors of the difference between 2009 and 2016 for each of the disturbances. Bird surveys were completed in each year from 2009 and species richness is shown only for the start (2009) and end (2016) of the study.

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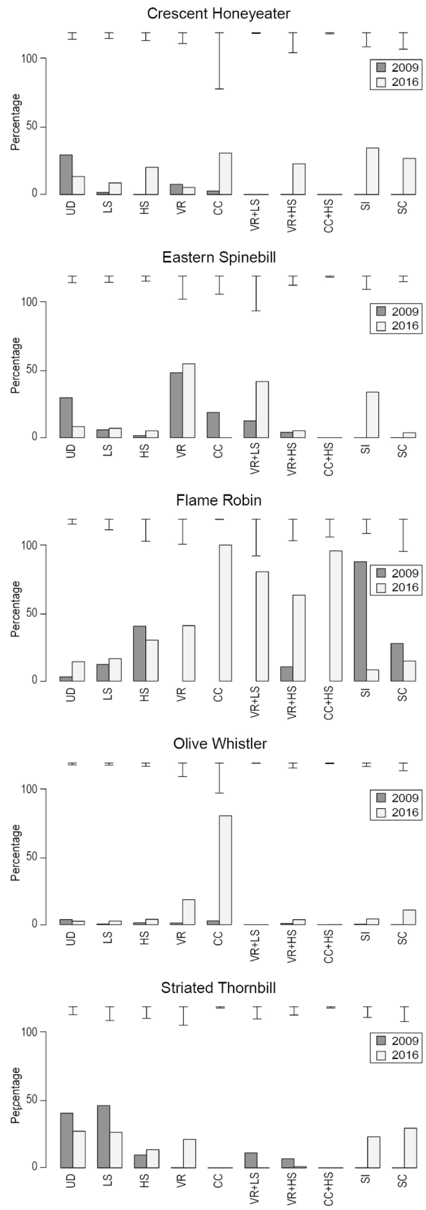

Fig. 4. Estimated effects of disturbance on percentage detection frequency in 2009 and 2016 for five individual bird species. Response patterns for other individual species of birds are shown in Fig. S1 in the supplementary material. The lines above the bars in the figure show the estimated standard errors of the difference between 2009 and 2016 for each of the disturbances. Bird surveys were completed in each year from 2009 and a subset of individual species responses are shown only for the start (2009) and end (2016) of the study.

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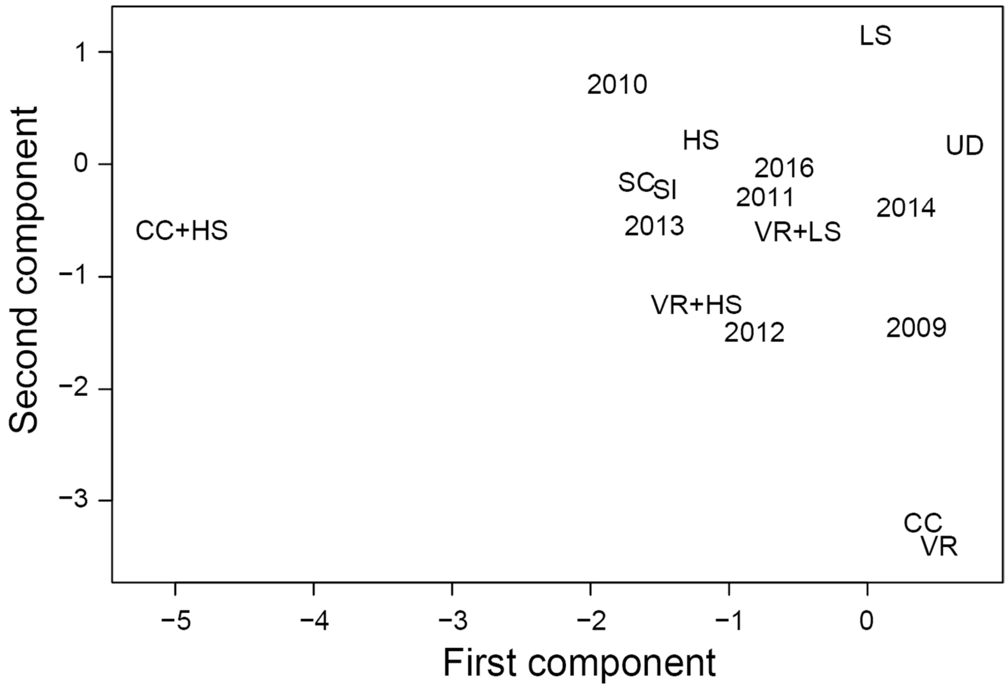

Fig. 5. First two components from canonical correspondence analysis showing scores (and therefore locations in multi-dimensional space) for the years in this study and ten types of disturbance examined in this study (see Table 1).

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SUPPORTING INFORMATION

Table S1. Summary of the life history and morphological traits used in the analysis, and the relationship of these traits with environmental change. *

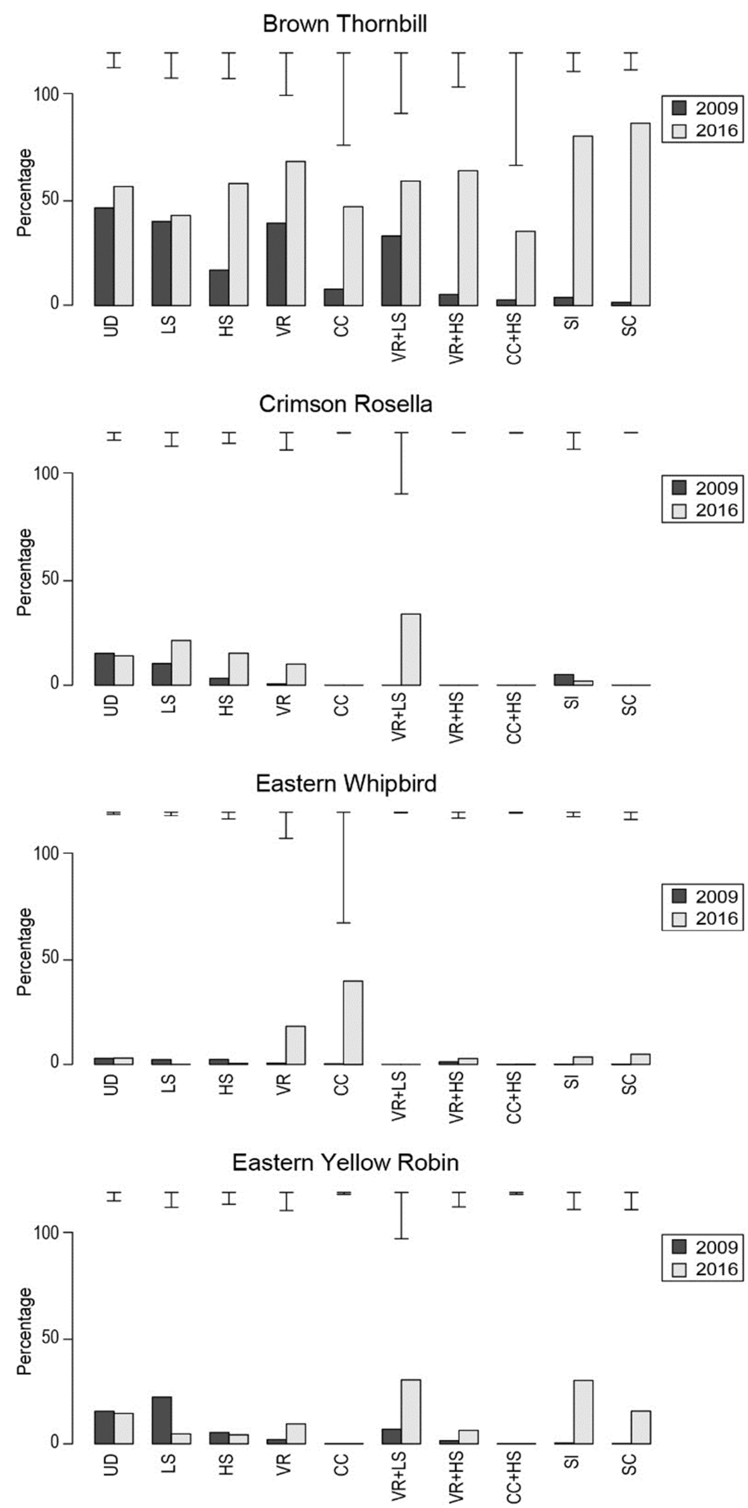
Trait	Levels/Definition	Relationship with environmental change*
Habitat	Forest, Open-woodland	Habitat generalists appear more resilient to environmental change as they have greater habitat use options.
Diet	Invertebrates, Nectar, Seeds, Varied	Influences all aspects of foraging behaviour. Birds with specialised diets are susceptible to environmental change that reduces primary diet.
Foraging substrate	Canopy, Understorey, Ground	Impacts all aspects of resource use by birds. Species with particular foraging behaviours may be impacted by environmental change.
Social system	Large flocks, Small flocks or solitary	Habitat loss and modification can disrupt social dynamics.
Reproductive effort	Clutch size multiplied by number of broods per season	Species with low reproductive rates (e.g. small clutch size, infrequent breeding and low annual productivity) and low survival rates are less resilient to environmental change (i.e. have a reduced capacity to recover from perturbations).
Migratory status	Dispersal/nomadic, Migratory, Sedentary	Birds with limited dispersal capacity (e.g. short distances or movements confined to certain vegetation types) may suffer more from reduced landscape connectivity.
Body mass	Log (body mass)	Strongly relates to a range of other traits in birds including metabolic rate, foraging behaviour, longevity and home-range size.
Wing morphology	Residuals from the linear regression: log(body mass) ~ log (wing length)	Aligned with movement capacity, which in turn influences resource use and the ability to respond to environmental change that disrupts landscape connectivity or reduces resource density.
Dispersal ratio	Cube root of the relationship between body mass and wing length	Linked with movement capacity.

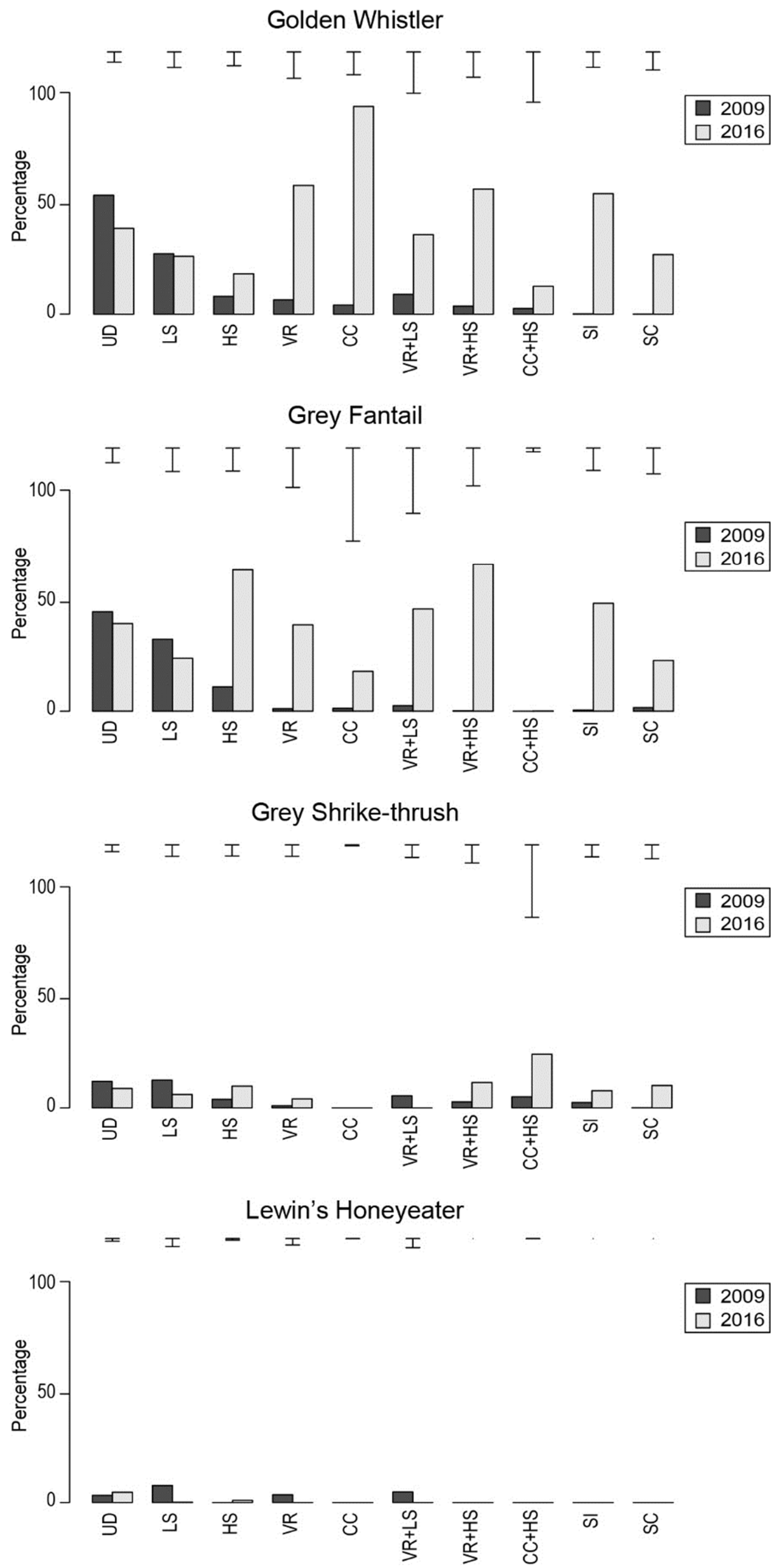
* Modified from Luck, G., Lavorel, S., McIntyre, S. & Lumb, K. (2012) Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, **81**, 1065-1076.

Table S2. Number of detections and number of site x year combinations with birds present for the most common species. Acronyms correspond to those used in canonical correspondence analysis in Fig. S2.

Species	**Acronym**	**Scientific name**	**No. of detections**	**Site x Year combinations**
White-browed Scrubwren	wbsw	*Sericornis frontalis*	1206	407
Brown Thornbill	btb	*Acanthiza pusilla*	1056	400
Grey Fantail	gfan	*Rhipidura albiscapa*	774	297
Golden Whistler	gw	*Pachycephala pectoralis*	691	281
Striated Thornbill	stb	*Acanthiza lineata*	511	240
Silvereye	seye	*Zosterops lateralis*	475	249
Flame Robin	frob	*Petroica phoenicea*	380	201
Crescent Honeyeater	che	*Phylidonyris pyrrhopterus*	311	145
Eastern Spinebill	esb	*Acanthorhynchus tenuirostris*	276	145
Striated Pardalote	stp	*Pardalotus striatus*	270	149
Crimson Rosella	cros	*Pardalotus striatus*	249	148
Eastern Yellow Robin	eyr	*Eopsaltria australis*	248	155
Spotted Pardalote	spp	*Pardalotus punctatus*	226	137
Grey Shrike-thrush	gst	*Colluricincla harmonica*	200	135
Yellow-faced Honeyeater	yfhe	*Caligavis chrysops*	144	89
Rufous Fantail	rft	*Rhipidura rufifrons*	111	66
White-throated Treecreeper	wttc	*Cormobates leucophaea*	109	79
Rose Robin	rrob	*Petroica rosea*	82	55
Eastern Whipbird	ewb	*Psophodes olivaceus*	80	50
White-eared Honeyeater	wehe	*Nesoptilotis leucotis*	80	44
Pilotbird	pb	*Pycnoptilus floccosus*	78	52
Olive Whistler	ow	*Pachycephala olivacea*	76	55
Lewin's Honeyeater	lhe	*Meliphaga lewinii*	62	46
Brown-headed Honeyeater	bhhe	*Melithreptus brevirostris*	59	46
Fan-tailed Cuckoo	ftc	*Cacomantis flabelliformis*	56	39
Superb Fairy-wren	sfw	*Malurus cyaneus*	56	39
Shining Bronze-Cuckoo	sbc	*Chalcites lucidus*	51	40
White-naped Honeyeater	wnhe	*Melithreptus lunatus*	40	21
Superb Lyrebird	slb	*Menura novaehollandiae*	37	28
Pied Currawong	pcw	*Strepera graculina*	33	28
Brush Cuckoo	brc	*Cacomantis variolosus*	31	24
Pink Robin	prob	*Petroica rodinogaster*	31	23
Grey Currawong	gcw	*Strepera versicolor*	29	25
Laughing Kookaburra	lkook	*Dacelo novaeguineae*	26	21
Red Wattlebird	rwb	*Anthochaera carunculata*	23	21

Fig. S1. Estimated effects of disturbance on percentage detection frequency in 2009 and 2016 for 18 individual bird species. The lines above the bars in the figure show the estimated standard errors of the difference between 2009 and 2016 for each of the disturbances. Bird surveys were completed in each year from 2009 and a subset of individual species responses are shown only for the start (2009) and end (2016) of the study.




Golden Whistler
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SI
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Grey Fantail
Percentage
100
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2009
2016
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CC
VR+LS
VR+HS
CC+HS
SI
SC
Grey Shrike-thrush
Percentage
100
50
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2009
2016
UD
LS
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VR
CC
VR+LS
VR+HS
CC+HS
SI
SC
Lewin's Honeyeater
Percentage
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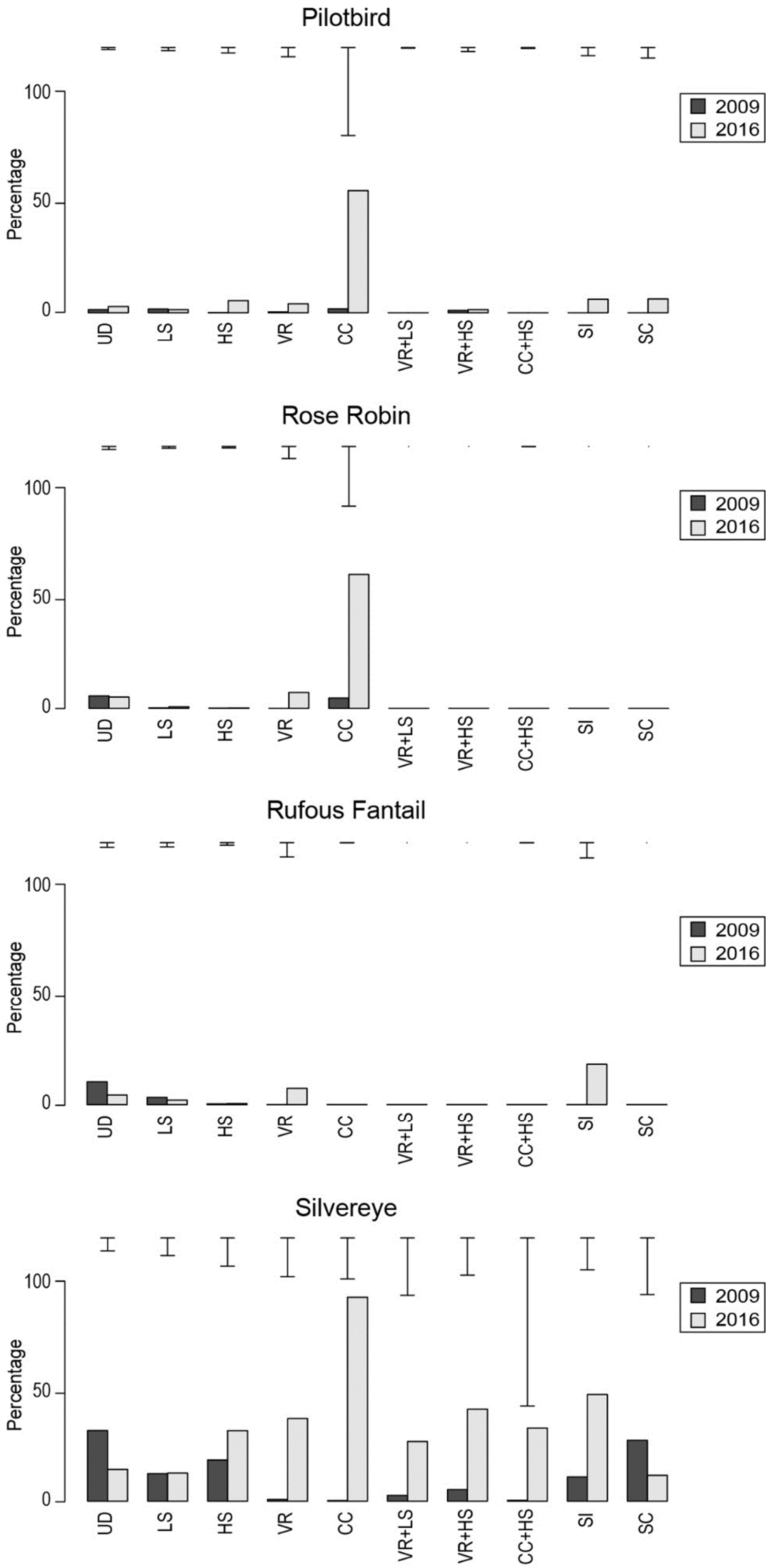
Pilotbird
Percentage
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UD
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VR+LS
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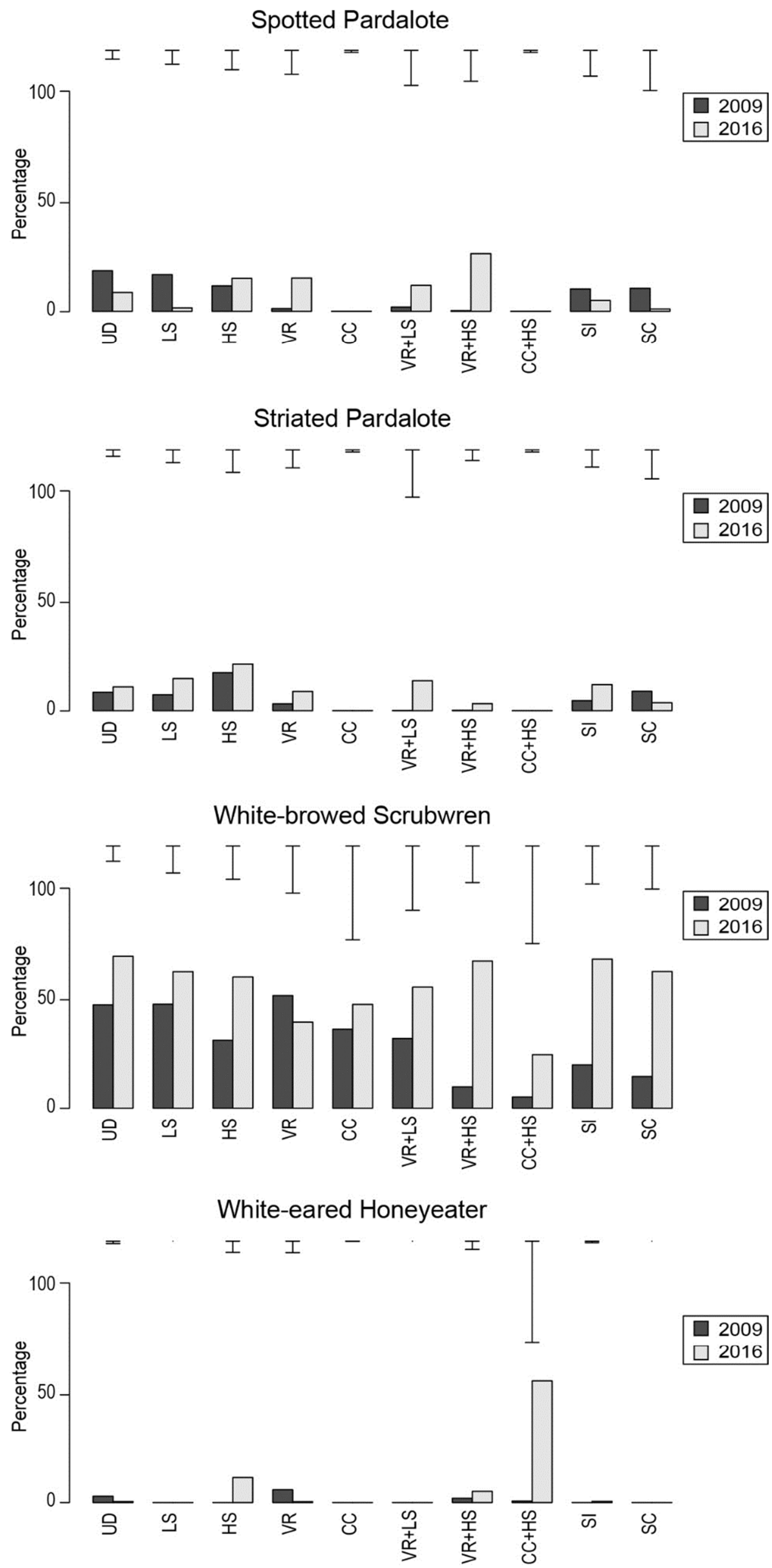
CC+HS
SI
SC
2009
2016
Rose Robin
Rufous Fantail
Silvereye


Spotted Pardalote
Percentage
100
50
0
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC
Striated Pardalote
Percentage
100
50
0
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC
White-browed Scrubwren
Percentage
100
50
0
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC
White-eared Honeyeater
Percentage
100
50
0
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC

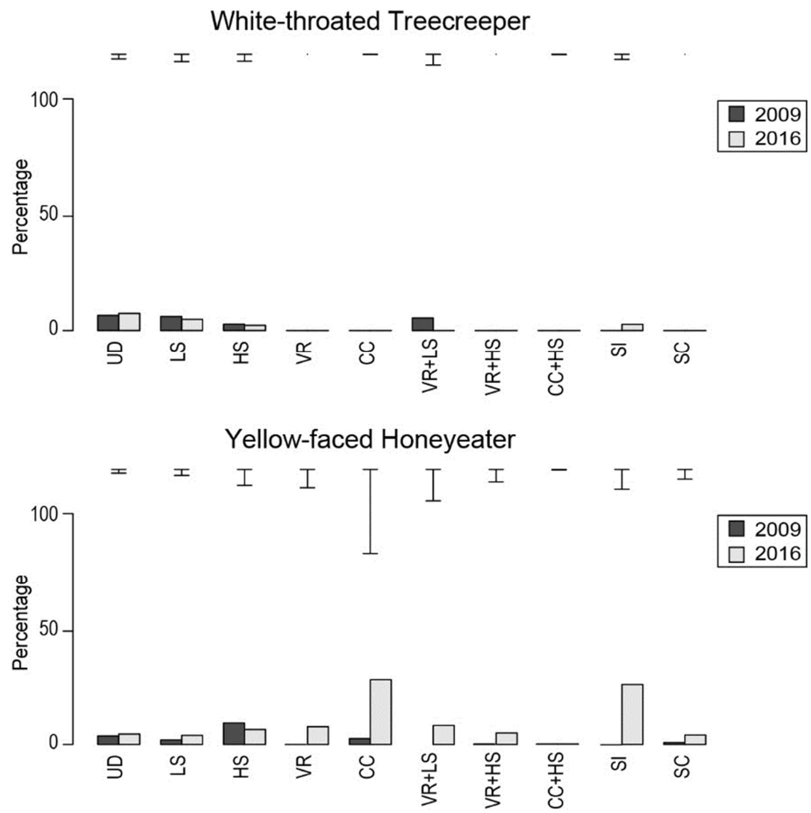

White-throated Treecreeper
100
50
0
Percentage
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC
Yellow-faced Honeyeater
100
50
0
Percentage
2009
2016
UD
LS
HS
VR
CC
VR+LS
VR+HS
CC+HS
SI
SC

Fig. S2. First two components from canonical correspondence analysis showing locations in multi-dimensional space for the 35 most common bird species. Acronyms for particular bird species are given in Table S2.